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# THE CONSTANTS OF THE SEMICIRCULAR CANAL DIFFERENTIAL EQUATION


Robert Mayne

Manager
Advanced Systems and Technologies Division



This report is in partial compliance to a contract under the

National Aeronautics and Space Administration
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## SUMMARY

The differential equation proposed by Steinhausen[10] for the response of the semicircular canals includes two constants which must be determined experimentally or computed from known canal characteristics. There is general agreement regarding the value of the ratio of the two constants, but wide differences regarding their actual values. This paper examines the evidence for the different values of these constants.

## INTRODUCTION

Steinhausen[10] defined the response of the semicircular canals by the equation,

$$\ddot{\theta} + L\dot{\theta} + P\theta = f(t) \tag{1}$$

where

$\theta$ = displacement of the endolymph

$L = \frac{\phi}{I}$   $P = \frac{\Delta}{I}$

and

$\phi$ = the moment of viscous force exerted on the endolymph per unit angular velocity

$I$ = the moment of inertia of the fluid

$\Delta$ = the elastic moment exerted on the endolymph per unit angular displacement.

The ratio $\frac{L}{P}$ is the time constant $\tau$ of the canals and has been established by various methods. There is general agreement between these methods which give a value of $\tau$ between 7 and 10 for the canals of man.

There is no such agreement, however, for the values of L and P. Van Egmond,[2] et al, and Niven and Hixson,[8] give approximate values of L = 10 and P = 1, while Mayne[7] found values of L = 200 and P = 24; Jones and Milsum[4] published frequency response of the canals corresponding to still higher values for these constants. The discrepancy is in the value of L, because P is not determined directly but computed from L and the time constant $\tau$. It is proposed to examine here the manner in which the constant L has been calculated.

# THE CONSTANT OF THE SEMICIRCULAR CANAL DIFFERENTIAL EQUATION

## Hydrodynamic Considerations

Schmaltz[9] was perhaps the first to apply mathematical analysis to the semicircular canals. His equation did not include the elasticity of the cupula, which was introduced by Steinhausen.[10] It included, however, the constant L. He computed L from the following formula which he derived from hydrodynamic considerations.

$$L = \frac{8\mu}{r^2 \ell} \tag{2}$$

where

$\mu$ = the coefficient of viscosity of the endolymph taken as $1 \times 10^{-2}$ gr/cm sec

$\ell$ = density of the endolymph taken as 1 gr/cm$^3$

r = internal radius of the semicircular canals taken as $2 \times 10^{-2}$ cm.

Using this formula and the above values for the characteristics of the endolymph and dimensions of the canals, Schmaltz[9] obtains,

$$L = 200.$$

Mayne[5] used this value of L, together with an estimated time constant of 8.3, to compute P = 24.

The same formula was used by van Egmond, et al,[2] with alteration, to compute L, and has been referred to frequently in the literature. Because of the discrepancy in the value of L computed by this formula and that proposed by various investigators, it is well to examine its derivation.

## Derivation of the Formula

The formula is based on the Hagen Poiseuille law for laminar flow in pipe. Laminar flow always occurs when the Reynold number is less than 2200. The Reynold number of the semicircular canal probably never exceeds one (1) or two (2) and, therefore, the canals are well within the range of application of the law.

From the laws of laminar flow of fluid in a tube[1] we have,

$$Q = \frac{\pi (P_1 - P_2)\, d^4}{128\, \mu \ell} = \frac{\pi (P_1 - P_2)\, r^4}{8\, \mu \ell} \tag{3}$$

where

$Q$ = volume of fluid delivered per unit of time

$P_1 - P_2$ = the difference of pressure between the two ends of the pipe

$\ell$ = the length of the pipe.

But,

$$(P_1 - P_2)\, \pi r^2 = f \tag{4}$$

where

$f$ = force exerted on the fluid.

Also,

$$v = \frac{Q}{\pi r^2} \tag{5}$$

where

$v$ = the velocity of the fluid.

Substituting Equations (4) and (5) in Equation (3) gives

$$v = \frac{f}{8 \pi \mu \ell} \tag{6}$$

but for the canal,

$$\ell = 2 \pi R \tag{7}$$

where

$R$ = the radius of curvature of the canal.

Substituting Equation (7) in Equation (6), and dividing by R to obtain angular velocity, we have

$$\dot{\theta} = \frac{f}{16\pi^2 r R^2} \quad . \tag{8}$$

Solving for the force on the endolymph per unit velocity gives

$$\frac{f}{\dot{\theta}} = 16\pi^2 \mu R^2 , \tag{9}$$

or, in terms of moment per unit velocity,

$$\frac{fR}{\dot{\theta}} = \Phi = 16\pi^2 \mu R^3 \quad . \tag{10}$$

The moment of inertia of the endolymph is

$$I = mR^2 \tag{11}$$

where

m = the mass of the endolymph,

giving,

$$I = 2\pi^2 r^2 R^3 \rho \tag{12}$$

where

$\rho$ = the density of the fluid.

Finally, from Equations (10) and (12),

$$L = \frac{\Phi}{I} = \frac{8\mu}{r^2 \rho} \quad , \tag{13}$$

which is the formula derived by Schmaltz. We will see later that there is an error or an omission in this derivation.

## The Effect of the Utricle

The formula is developed under the assumption that the canals form a complete circle of the same internal radius. Actually, as their name implies, the canals comprise only about half a circle; the remaining half is taken up by the utricle where the canal is very much enlarged and consequently the flow is very much slower. Van Egmond, et al,[2] argued that because of the reduction of velocity in the utricle, the viscosity can be neglected and the constant eight (8) in Equation (13) should be reduced to four (4).

There is no question that viscosity can be neglected in a channel many times the cross section of the canal. But there is a compensating factor to this reduction of viscosity. The mass can also be neglected. The kinetic energy of the flow is proportional to the square of the velocity times the mass. If velocity is reduced in the same proportion as mass is increased, there is a reduction of energy. If, for instance, the cross section of the canal is increased one hundredfold in the utricle (and the cross section is probably increased by a much greater factor), the velocity is decreased and the mass of the flow increased by the same ratio. The net effect will be to reduce the kinetic energy by a factor of 100. We can say, then, that the effective mass in the utricle is one percent that of a comparative length of canal, or 0.01 percent of the mass of fluid flow in the utricle.

It may be argued that during angular acceleration the same pressure is built up per unit length, regardless of the size of the channel and, therefore, that the enlarged channel should contribute to the driving force on the fluid in the same manner as any other section of the canal. As soon as flow starts, however, the fluid must be accelerated at the entrance of the canal from the utricle and the pressure will be lost. The pressure built up in the utricle contributes a negligible amount in driving the endolymph in the canals.

It will be noted that the radius of curvature of the canals, or its length, does not enter into Formula (13). The value of L is independent of what proportion of canal is taken up by the utricle. The reduction of the constant from eight to four as proposed by van Egmond, et al, is not justified, therefore, on the ground of the reduced velocity in the utricle. It is justified, however, on other grounds.

## The Effect of Parabolic Distribution of Velocity in the Canals

The distribution of velocity across the diameter of a tube is not constant for laminar flow. This distribution is taken into account in Equation (3) insofar as the volume of fluid delivered by the pipe is concerned. The linear velocity in Equation (5) and the angular velocity $\dot{\theta}$ in Equation (8) are average velocities. The average angular velocity of the endolymph integrated with respect to time is a true measure of the cupula displacement.

The average velocity, however, cannot be used in the computation of inertial forces. Equation (1) is derived on the basis of an equilibrium between inertial, viscous, and elastic forces, or, amounting to the same thing, by an accounting of all energies in the way of the kinetic energy of the fluid, the potential energy of the displaced cupula, energy losses through viscosity, and energy input through transient movements of the head. The derivation implies that the energy of the flow is

$$\varepsilon = \tfrac{1}{2}mv^2$$

where

$\varepsilon$ = the kinetic energy of the flow of the endolymph
$m$ = the mass of the endolymph
$v$ = the linear velocity.

But this formula does not give the true value of $\varepsilon$ if the average velocity is used. To obtain the true value, an integration must be performed of the product of incremental masses of endolymph by half the square of their velocity. The difference can be corrected by using an effective mass different from the actual one. We will estimate the factor by which the actual mass must be multiplied to obtain the proper value of the effective mass.

As indicated above, the distribution of velocity across the diameter of a pipe is parabolic for laminar flow. It is zero at the wall and a maximum at the center. Let us express the velocity by the formula

$$v = a(R_p^2 - r^2) \tag{14}$$

where

$v$ = velocity of the fluid at a distance r from the center
$R_p$ = the internal radius of the pipe
$a$ = a constant as a function of viscosity.

The equation fulfills the condition of parabolic laminar flow with zero velocity at the wall and maximum velocity at the center. We will first derive the kinetic energy of the flow per unit time as computed wrongly from average velocity.

The flow per second computed on the basis of Equation (14) is

$$Q = \int_o^{R_p} (2\pi r\, dr)\, a(R_p^2 - r^2) \tag{15}$$

$$Q = 2\pi a \int_o^{R_p} (R_p^2 - r^2)\, r dr$$

$$Q = \frac{\pi a}{2} R_p^4 \quad . \tag{16}$$

The average velocity $v_a$ is given by

$$v_a = \frac{Q}{A} \tag{17}$$

where A is the internal area of the pipe, and,

$A = \pi R_p^2$

and, therefore,

$$v_a = \frac{\pi a}{2} \frac{R_p^4}{\pi R_p^2} = \tfrac{1}{2} a R_p^2 \quad . \tag{19}$$

The kinetic energy $\dot{\varepsilon}_\omega$ per second computed, wrongly, on the basis of average velocity would be

$$\dot{\varepsilon}_\omega = \tfrac{1}{2} Q \rho v_a^2 \quad , \tag{20}$$

or, from Equations (16) and (19),

$$\dot{\varepsilon}_\omega = \tfrac{1}{2} \rho \frac{\pi a R_p^4}{2} \left(\tfrac{1}{2} a R_p^2\right)^2 \tag{21}$$

$$\dot{\varepsilon}_\omega = \frac{1}{16} \rho \pi a^3 R_p^8 \quad . \tag{22}$$

We next compute the correct kinetic energy $\dot{\varepsilon}_c$ of the flow by integrating the product of the flow at each increment of radius by half the velocity squared at the same point. The flow per second for an increment of radius dr is

$$dQ = (2 \pi r \, dr) \, v_r \tag{23}$$

$$dQ = (2 \pi r \, dr) \, a(R_p^2 - r^2),$$

and the increment of energy is

$$d\dot{\varepsilon}_c = \tfrac{1}{2} \rho (2 \pi r \, dr) \left[a(R_p^2 - r^2)\right] \left[a(R_p^2 - r^2)\right]^2 \tag{25}$$

and, therefore,

$$\dot{\varepsilon}_c = \rho \pi a^3 \int_0^{R_p} (R_p^2 - r^2)^3 \, r \, dr$$

$$\dot{\varepsilon}_c = \frac{1}{8} \rho \pi a^3 R_p^8 \quad . \tag{27}$$

From Equations (22) and (27), it is seen that

$$\dot{\varepsilon}_c = 2 \, \dot{\varepsilon}_\omega \quad . \tag{28}$$

To correct for this effect we must double the value of $\rho$ in Equation (13) and the equation becomes

$$L = \frac{4\mu}{r^2 \rho} \quad . \tag{29}$$

This is the same equation used by van Egmond, et al,[2] but derived on other grounds.

<u>Check of the Formula</u>

Schmaltz used a value of r = 0.02 cm for the internal radius of the canals of man. A more accurate figure appears to be about 0.014, so that if this dimension is used in the modified formula, the value of L = 200 remains approximately the same.

Van Egmond, et al,[2] applied the formula to compute the constant L for the canals of man in an attempt to confirm the value of 10 derived by other means. They used a value of 0.006 for the coefficient of viscosity instead of 0.01 used by Schmaltz.[9] This would have the effect of reducing the constant. In addition, they took the radius of the canal to be r = 0.030 cm, whereas, as indicated earlier, the presently accepted value is about r = 0.014. On this basis they obtained a value of L = 27. Had the previously accepted value of r been used, the result would have been L = 120 and 200 with a coefficient of viscosity of 0.01.

A check of the formula may be made on the basis of experimentally derived L for the ray. In a series of carefully conducted experiments, Groen, et al,[3] derived the value of L = 35 for the elasmobranch horizontal semicircular canals on the basis of measurements of the electrical activity of single fibers. Considerable reliance can be placed on the validity of the value of L. The internal radius squared of the ray is given by Jones and Spells[4] as $r^2 = 0.11\ \text{mm}^2$. Assuming this dimension corresponds to that of the canals tested by Groen, et al,[3] the value of L computed from Formula (29) would be

$$L = 36 \quad . \tag{30}$$

This is a rather remarkable agreement between theory and experiment. The agreement is probably too good not to involve some compensating errors. Still, it lends weight to the likely validity of the formula.

Experimental Derivation of L by van Egmond, et al.[2]

Van Egmond, et al,[2] argued very properly that cupula displacement, and, therefore, sensed velocity, lead actual motion for frequencies below the natural frequency of the system and lag for frequencies above. If, therefore, a subject would signal the instant at which he sensed the velocity to be a maximum for variable frequencies of oscillation, the natural frequency would be one between an observed lead and lag. P could then be computed from this value by the formula

$$\omega_o^2 = P \tag{31}$$

and L determined from

$$L = P\tau \ . \tag{32}$$

In carrying out their experiments, van Egmond, et al,[2] used the ingenious technique of allowing the oscillation to die out gradually so that only the maximum velocity portion of the cycle would be above threshold. The frequencies at which lead and lag were noted were, respectively, 1.08 and 1.57 radians/second, or 0.189 and 0.25 cps, from which they determined $\omega_o$ = 1.25 radians/second. The phase lead and lag for these two frequencies can be computed from the formula

$$\tan \delta = \frac{\omega_o^2 - \omega^2}{\omega L} \tag{33}$$

Using the value of L = 10 determined by van Egmond, et al,[2] on the basis of these observations, we have

$$\delta_1 = 2.1^{\circ}$$
$$\delta_2 = 3.2^{\circ}$$

where $\delta_1$ is the lead for a frequency of 0.189 cps and $\delta_2$ is the lag for a frequency of 0.25 cps.

At these frequencies the time difference between the sensed point of maximum velocity and the actual point is about 0.035 second. The subjective detection of such small time differences would appear difficult. These time differences would be 20 times shorter if the value of L were taken to be 200 as computed from Equation (29).

Subjective observations may be distorted by a number of factors. There is, first, the reaction time delay which is normally an order of magnitude greater than the required accuracy. There is, also, the hypothetical shift of sensed body axis which is greatest at high velocity. It would appear, therefore, that the values determined by van Egmond, et al,[2] are open to question.

Determination of the Value of L by Niven and Hixson[8]

Niven and Hixson[8] computed L on the basis of a series of excellent experiments relating the phase shift of nystagmus to an impressed sinusoidal motion for the steady state. Their method is not open to the same objections as that of van Egmond. In the first place, the measurements are objective and do not introduce the problem of reaction time delay or shift of sensed body axis. In the second place, the measurements of phase are taken at zero velocity, eliminating errors due to leading eye movements. There remains, however, a problem of the possible accuracy of phase measurement.

Niven and Hixson[8] realized that the accuracy of the determination of L required the use of the highest possible frequency of oscillation. In a highly damped system, such as the semicircular canals, the response at low frequency is affected mostly by the time constant, while the value of L affects mainly the response at high frequencies. Niven and Hixson,[8] however, were probably limited by their equipment to a maximum frequency of 0.2 cps. It can be computed that at this frequency an error of measurement of about four degrees would account for the discrepancy between a value for L of 16 such as found in these experiments and one of 200. Some doubts are permitted whether or not the nystagmus follows vestibular signals to this degree of accuracy, assuming methods of measurement are adequate.

The Effect of Cupula Leakage

In order to explain the discrepancy between their computed value of 27 and an experimentally derived value of 10 for L, van Egmond, et al,[2] assumed that leakage did occur between the cupula and the walls of the ampulla. It is, therefore, desirable to investigate the effect of such leakage on the values of the constants of the equation.

Figure 1 illustrates diagrammatically a canal with a leaky cupula.

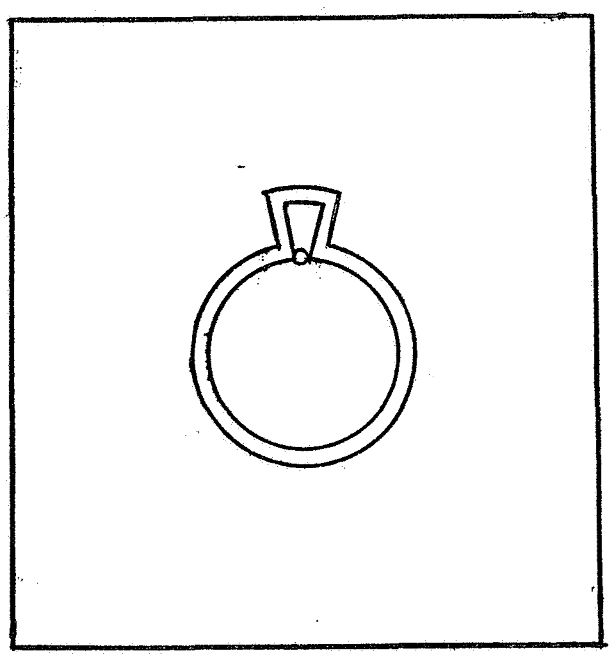

Figure 1. Schematic representation of leaky cupula.

We let:

$\theta_e$ = endolymph displacement with respect to the walls

$\theta_c$ = cupula angular displacement where $\theta_e$ is assumed equal to $\theta_c$ for the case of zero cupula leakage

$\Phi_1$ = viscous moment on endolymph per unit velocity of endolymph

$\Phi_2$ = viscous moment on endolymph per unit velocity of cupula

$\Delta$ = elastic force on endolymph per unit deflection of cupula

I = the effective moment of inertia of the endolymph and of all other mass in the system.

For the sake of simplicity, we consider the case without input head movements. Values of constants estimated on this basis would obviously be the same as would be derived with a forcing function.

$$I\ddot{\theta}_e + \Phi_1\dot{\theta}_e + \Phi_2 (\dot{\theta}_e - \dot{\theta}_c) = 0 \tag{34}$$

$$\Delta\theta_c = \Phi_2 (\dot{\theta}_e - \dot{\theta}_c) \ . \tag{35}$$

Equation (34) expresses the fact that viscous forces and inertial forces should add up to zero around the loop. Equation (35) states that cupula deflection is proportional to the difference of force between the two opposite walls of the cupula.

Solving Equation (35) for $\dot{\theta}_e$,

$$\dot{\theta}_e = \dot{\theta}_c + \frac{\Delta}{\Phi_2}\theta_c \tag{36}$$

differentiating Equation (36) with respect to time,

$$\ddot{\theta}_e = \ddot{\theta}_c + \frac{\Delta}{\Phi_2}\dot{\theta}_c \ . \tag{37}$$

Substituting Equations (35), (36), and (37) in Equation (34) makes it possible to eliminate $\theta_e$, giving

$$\ddot{\theta}_c + \left(\frac{I\Delta}{\Phi_1 \Phi_2} + 1\right) \frac{\Phi_1}{I} \dot{\theta}_c + \left(\frac{\Phi_1}{\Phi_2} + 1\right) \frac{\Delta}{I} \theta_c = 0 \tag{38}$$

or, in terms of L and P, as defined previously,

$$\ddot{\theta}_c + \left(\frac{I\Delta}{\Phi_1 \Phi_2} + 1\right) L\dot{\theta}_c + \left(\frac{\Phi_1}{\Phi_2} + 1\right) P\theta_c = 0. \tag{39}$$

If there is no leakage on the cupula, the value of $\Phi_2$ is infinite and the equation becomes

$$\ddot{\theta}_c + L\dot{\theta}_c + P\theta_c = 0, \tag{40}$$

which is equivalent to Equation (1) without a forcing function and the case where $\theta_e = \theta_c$. The latter assumption does not affect the qualitative results of the analysis, which shows that the effect of cupula leakage is to increase the values of L and P. Cupula leakage cannot be invoked, therefore, to account for a reduction of L computed on the basis of no leakage. The effect is opposite.

Functional Requirement

The value of L defines the limits of high frequency response for the canal. The so-called high corner frequency is given by the formula

$$f_u = \frac{L}{2\pi} \text{ cps.} \tag{41}$$

This gives a value for man of

$$f_u = 32 \text{ cps for } L = 200$$
$$f_u = 1.6 \text{ cps for } L = 10.$$

The upper corner frequency is a point in the frequency response curve where the phase shift is 45 degrees and the amplitude ratio is 0.707. A component of a system operating at its corner frequency would produce considerable distortion. A control engineer designing a reasonably accurate system would certainly pick a value of ten to one between upper corner frequency of a component and the over-all desired response of the system. The value of L = 200 would, therefore, be satisfactory for a frequency response of 3 cps, which appears to be within the bandwidth of head motion. A corner frequency of 1.6 cps would seem totally inadequate.

It is, of course, dangerous to reason teleologically when we do not know the exact configuration of the system. Still, it appears that better high frequency response is called for the semicircular canals than can be provided by a canal with an upper corner frequency of 1.6 cps.

The Adaptation of the Canals to Various Species

That the high frequency response of canals is defined by L and, therefore, by $\frac{1}{r^2}$, as indicated by Equation (29), is shown by a study of the adaptation of canals to various species (Jones and Spells,[4] and Mayne[6]). Systematic variations of r are indicated by these studies to correspond to estimated variations in the frequency of body movements of different species.

Deflection of the Cupula

The endolymph displacement is given by

$$\theta_o = \frac{\dot{\theta}_i}{L} \frac{1}{\sqrt{\left(\frac{P - \omega^2}{L\omega}\right)^2 + 1}}, \tag{42}$$

for a frequency within the bandwidth of the canal where

$$P = \omega_o^2 \text{ apx.}$$

$$\theta_o = \frac{\dot{\theta}_i}{L}$$

where

$\theta_o$ = endolymph displacement output

$\dot{\theta}_i$ = velocity of the head.

If we assume that an average maximum velocity of the head is $500^o$/sec, the maximum deflection of the endolymph would be

$$\theta_o = \frac{500}{200} = 2.5^o \quad \text{for } L = 200$$

and

$$\theta_o = \frac{500}{10} = 50^o \quad \text{for } L = 10.$$

Not enough data are available regarding the size of canals and cupula to compute the corresponding amount of cupula deflection. It may be expected that it would be less, but assuming, with van Egmond, that cupula deflection is the same as that of the endolymph, it will be seen that the two constants correspond to widely differing deflections of the cupula. In view of the small amount of deflection required by the basal membrane for adequate stimulation of the auditory nerves in the cochlea, it would appear that the lower deflection would be sufficient. Measurement of endolymph displacement for given velocity input at frequencies within the bandwidth of the system may provide a means to evaluate the constant L.

## Discussion

As long as vestibular research deals mainly with low frequency phenomena, as in cupulometry or post-rotational reactions, the knowledge of the time constant of the canals is sufficient. As research proceeds to the investigations of the part played by the canals in the control of body movements, it becomes necessary to know the actual value of the canal constants in addition to their ratio. Experimentally derived values differ by an order of magnitude from those computed theoretically. It is difficult to see what could be wrong with the theoretical derivation, particularly when it fits carefully, experimentally derived values for the canals of the elasmobranch and is consistent with observed variations of canal dimensions in various species. New experimental methods are needed to resolve the differences. These experiments must make use of frequencies higher than used previously. Nystagmus may not be a suitable variable to observe as an output of the vestibule. It could be that the constants will have to be derived on the basis of analysis of movements demonstrated to occur in response to vestibular signals. But there, again, the mode of response of body control must first be established. It cannot be assumed that the vestibule operates directly in closed loop control in body control. The more sophisticated system of programming must be taken into account. In the meantime, without more data, it would seem that the weight of evidence favors the higher valued constants.

# REFERENCES


1. Dodge, R A and Thomson, M J, Fluid Mechanics. McGraw-Hill Book Company, Inc. (New York, N Y, 1937), Chapt VIII, p 171.

2. van Egmond, A A J, Groen, J J and Jongkees, L B W, The Mechanics of the semicircular canal. J Physiol 110, 1-17, 1949.

3. Groen, J J, Lowenstein, O, and Vendrik, A J H, The mechanical analysis of the responses from the end organs of the horizontal semicircular canal in the isolated elasmobranch labyrinth. J Physiol, 117, 329-346, 1952.

4. Jones, G M and Spells, K E, A theoretical and comparative study of the functional dependence of the semicircular canal upon its physical dimensions. Proc Royal Soc, B Vol 157, 403-419, 1963.

5. Mayne, R, The dynamic characteristics of the semicircular canals. J Comp Physiol Psychol, Vol 43, No. 4, August 1950.

6. Mayne, R, Functional aspects of the system of spatial representation in the control of body movements. I. Over-all considerations. Goodyear Aerospace Corp., GERA-1056, 23 Aug 1965.

7. Mayne, R, Nystagmus and body control for inputs of repeated patterns. Goodyear Aerospace Corp., GERA-1080, 6 Oct 1965.

8. Niven, J I and Hixson, W C, Frequency response of the human semicircular canals: I. Steady-state ocular nystagmus response to high-level sinusoidal angular rotations. USN SAM/NASA Joint Report No. 58, Project MR005.13-6001, March 1961.

9. Schmaltz, G, The physical phenomena occurring in the semicircular canals during rotatory and thermic stimulation. Proc Royal Soc of Med Section of Otology, Vol 25, 359-381, 1 May 1931.

10. Steinhausen, W, Uber die Boebachtung der Cupula in den Bogengangsampullen des Labyrinths des lebenden hechts. Pflug Arch Ges Physiol, 232, 1933.